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Sperm competition in European water frogs

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Sperm from *Rana lessonae* was mixed with sperm from *Rana ridibunda* or *Rana* kl. *esculenta*. Eggs from *Rana lessonae* or *Rana ridibunda* were introduced into sperm suspensions producing progeny with *Rana lessonae*, *Rana* kl. *esculenta*, or *Rana ridibunda* phenotypes. Spermatozoa with *Rana lessonae* genomes always fertilized many more eggs than those with *Rana ridibunda* genomes.

INTRODUCTION

Central Europe is inhabited by three forms of water frogs: *Rana ridibunda* Pallas, 1771 and *Rana lessonae* Camerano, 1882, two Mendelian species, and *Rana* kl. *esculenta* Linné, 1758, a hybridogenetic hybrid between the two (BERGER, 1988 a; GRAF & POLLS PELAZ, 1989). Gametes of hybrids usually contain genomes of one of their parental species and genomes of the other species are excluded from the germ line premeiotically (UZZELL, HOTZ & BERGER, 1980; TUNNER & HEPPICH, 1981). In the Poznań region of Poland the sperm of *Rana* kl. *esculenta* contains the *Rana ridibunda* genome (UZZELL & BERGER, 1975).

In Central Europe, water frogs usually breed in May with the males appearing first at the breeding site. Their distribution at the breeding arena is not random (BLANKENHORN, 1977): in mixed *Rana lessonae* – *Rana esculenta* populations (L-E system, UZZELL & BERGER, 1975) most *Rana* kl. *esculenta* males gather in the center of the arena, while *Rana lessonae* males gather along the margins. All males compete for females, but *Rana lessonae* males have a higher probability for successful pair formation. All pairs in amplexus wander to the center of the arena (BLANKENHORN, 1977; BERGER & RYBACKI, pers. obs.) where they release gametes and further competition between spermatozoa may take place.

Our knowledge of sperm competition in Amphibia is confined to species with internal fertilization (HALLIDAY & VERRELL, 1984; HOUCK & SCHWENK, 1984). There are no published data on sperm competition between Amphibia with external fertilization, although it is likely to occur in foam-nesting frogs of the family Rhacophoridae (FUKUYAMA, 1991).

MATERIAL AND METHODS

Five females and ten males provided gametes for crossing experiments (Table I) carried out according to standard methods (BERGER, 1988 b) during the breeding time of water frogs. Males were killed and both testes were carefully crushed in equal volumes of aged tap water in separate petri dishes; spermatozoa were very mobile and always in masses. The testes of *Rana ridibunda* were approximately three times larger (about 120 mm^3) than those of *Rana lessonae* (about 40 mm^3), and those of *Rana* kl. *esculenta* were intermediate. Sperm suspensions of two selected males were poured into one dish and mixed, and ovulated eggs of *Rana lessonae* or *Rana ridibunda* were then squeezed into this mixture. In cross 6x/91 we used 131 eggs from *Rana lessonae* and 141 eggs from *Rana ridibunda*. When larvae reached stage 25 (SHUMWAY, 1940), numbers of survivors were assessed and many of them were reared further in aquaria and basins outdoors. After metamorphosis, all progeny were killed and preserved in 3 % formalin. Their genotype was inferred from morphological phenotype (BERGER, 1964; BERGER, ROGUSKI & UZZELL, 1978).

Table I. – Viability and genomic composition of water frog progeny.

Parents. – N/y: successive number of female (N) and year of laying the eggs (y); letters designate the male (or males) used in crosses with the same female; les: *Rana lessonae*; rid: *Rana ridibunda*; esc: *Rana* kl. *esculenta*.

Tadpoles. – N: number of individuals; survived: survived to the end of experiment; phenotype of the progeny: LL, *lessonae*, RL, *esculenta*, RR, *ridibunda*.

Parents			Progeny		Rearing of tadpoles						
N/y	Mothers	Fathers	Eggs	First cleavage %	Stage 25 %	N	Survived N	Phenotype Number LL	RL	RR	Ratio of sperm genomes L : R
2/77a	les1	les1 + rid1	945	98.0	88.6	185	149	129	20		6 : 1
2/91l	les3	les3 + rid2	241	99.2	88.4	113	87	59	28		2 : 1
3/91c	rid1	les3 + rid2	349	99.1	97.4	140	123		106	17	6 : 1
3/90k	les2	les2 + esc1	145	92.4	22.1	32	30	28	2		14 : 1
2/91m	les3	les3 + esc2	287	99.3	76.7	220	153	149	4		37 : 1
3/91d	rid1	les3 + esc2	331	99.1	97.0	120	114		114		114 : 0
3/91g	rid1	les4 + esc3	191	99.5	85.9	164	127		123	4	31 : 1
6x/91	les4 + rid1	les4 + rid3	272	100.0	94.5	158	147	56	91		? : ?
3/91b	rid1	rid3	103	100.0	97.1	—					



RESULTS AND DISCUSSION

Egg cleavage and zygote viability was very high in all crosses except one (cross 3/90k). The progeny in all crosses contained many more individuals fathered by *Rana lessonae* than those fathered by *Rana ridibunda* or *Rana* kl. *esculenta*. Spermatozoa with *ridibunda* genomes (R) fertilized eggs with *lessonae* genomes (L) more frequently than eggs with *ridibunda* genomes (R). *Rana ridibunda* individuals (RR) were not numerous or even absent in the progeny.

Cross 6x/91 exemplifies this phenomenon. Given nearly equal numbers of ova (131:141) and assuming equal chances of fertilization by sperm of *Rana lessonae* and *Rana ridibunda*, the expected ratio of LL:RL:RR offspring in this cross should be approximately 1:2:1; there were, however, only progeny with *lessonae* (LL) and *esculenta* (RL) phenotypes in the 147 individuals, in a ratio of about 1:2 (56:91). Cleavage of all eggs and very high viability of offspring in cross 6x/91 suggests that individuals which might have received a R genome each from both parents were not eliminated during development. The very high viability of zygotes derived from the same *Rana ridibunda* pair, which developed in a separate petri dish (cross 3/91b), shows that both parents were normal and capable to create *Rana ridibunda* (RR) individuals. Scarcity of RR progeny is even more surprising because *Rana ridibunda* males and their testes were about three times larger than *Rana lessonae* ones and contained about three times more gametes (BERGER & RYBACKI, unpubl.). At present we cannot explain the causes underlying this phenomenon, but we assume that it is connected with the presence of *Rana lessonae* gametes in the sperm suspension.

Our data from all other crosses corroborate this conclusion. In three crosses (3/91c, 3/91d, 3/91g), about 50 % of *ridibunda* (RR) individuals are expected for equal numbers of spermatozoa with *lessonae* (L) and *ridibunda* (R) genomes and random fertilization, but the RR genotype appeared in only two crosses and in low frequency. Activity of spermatozoa with R genomes apparently is connected with their origin: spermatozoa of *Rana ridibunda* males fertilized more eggs (13.3-32.2 %) than spermatozoa of *Rana* kl. *esculenta* males (0-6.7 %) which also contain *ridibunda* (R) genomes (BERGER, 1988 a).

CONCLUSION

The European water frogs are promising objects for studies on gamete competition. All crosses between Mendelian forms in this group are easily achieved and give viable progeny with characters intermediate between parental types (BERGER, HOTZ & UZZELL, unpubl.). It is easy to determine their genetic origin from morphology (BERGER et al., 1978, 1982, 1986) or from electrophoresis (HOTZ & UZZELL, 1982). We anticipate that further studies will promote understanding of the mechanisms responsible for gamete competition.

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The amphibian fauna of the French Upper-Rhône floodplain. The Lavours marsh and the Jons sector

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The amphibian fauna of two sectors of the French Upper-Rhône was investigated at 38 sites. These sectors and sites were chosen to represent the braided or anastomosed floodplain. Among the 14 taxons inhabiting this district, 11 bred within the floodplain. The most constant taxons were *Triturus helveticus*, *Rana dalmatina* and *Rana* synkl. *esculenta*. *Bufo calamita*, *Hyla arborea* and *Pelodytes punctatus* were observed mainly in temporary sites in the vicinity of the active channel. *Bombina variegata* occurred in shallow overforested sites at the border of the floodplain. The distribution of taxons is discussed in connection with the patch dynamics concept.

INTRODUCTION

Although European amphibian communities in agrosystems are relatively well known (STRIJBOSCH, 1979; PAVIGNANO, GIACOMA & CASTELLANO, 1990), information on those that inhabit floodplains is still scarce. Floodplains are of great interest in understanding determinants of amphibian occurrence. In floodplain sectors where the geomorphology of the valley makes meandering possible, the diversity of aquatic sites may be very high (AMOROS et al., 1987, 1988). Diversity concerns both site configuration and the modes of water retention. Amphibian breeding sites are mainly semi-aquatic or permanent, with standing water or low current velocity. The semi-aquatic sites may originate according to three different processes (AMOROS, RICHARDOT-COULET & PAUTOU, 1982). Firstly, depressions may be formed in pebble beds or in alluvial side bars by the mechanical erosion of floods (or by human excavation). The bottom of such sites is not silted and water is retained for rather short periods (some weeks). The second group includes old oxbow lakes ("parapotamon" of AMOROS, RICHARDOT-COULET & PAUTOU, 1982), which have been partially filled with alluvium or autogenic organic matter. Their silted bottom retains water for several months. The third group includes marshes, which are the last stage of transition towards terrestrial habitat. Depending on water table level, water may be found more or less permanently in local depressions. Oxbow lakes, man-made excavations for peat extraction or drains are permanent aquatic sites, which may host breeding amphibians.

The terrestrial surroundings of these different kinds of sites also vary greatly (PAUTOU et al., 1985). In the French Upper-Rhône alluvial valley (south-eastern France), sites situated in pebble beds are mainly surrounded by moorland with *Phalaris arundinacea*, *Salix alba* and *Alnus incana*. Several species of *Salix*, *Alnus incana*, *Populus nigra* and *Quercus robur* characterize the alluvial forest on the side bars. The marshes are most often peat-moors colonized by *Alnus glutinosa*. The main system investigated in the present study was the Lavours marsh. We compared the amphibian fauna of this marsh with that of more juvenile sites situated in the braided sector of Jons. In this sector, the sites sampled were a connected oxbow lake and more or less temporary ponds located in alluvial side bars near the stream.

MATERIAL AND METHODS

STUDY DITES

The Lavours marsh

The Lavours marsh (fig. 1) is located 70 km downstream from Geneva. It occupies a 1200 ha hollow between the rivers Rhône and Séran just upstream from their confluence. The present description briefly summarizes the detailed ecological and historical studies by AÏN & PAUTOU (1969), BRAVARD (1987) and PAUTOU et al. (1991). The marsh originated in a post-glacial lake. This lake was progressively filled with sediment. When the Rhône breached through the moraine at Massignieu, the water level decreased, leading to a great productivity of the vegetation along the lake shores. Both sediment and peat then filled the northern part of the lake (the peat layer is 8 metres thick in the centre of the marsh). The lake was reduced until it reached its present shape, that of the present Lake Bourget, south of the marsh. Water flow from the river to the marsh was checked by man-made embankments, mainly erected during the XIXth century. The marsh is now overflowed only in decennial floods, when the discharge of the Rhône reaches 1500 m^3/s. The flow regime is of nival type, with high water in spring, whatever the amount of rain. Water from the Séran is then pushed back by the high level of the Rhône and floods the western border of the marsh. Such repeated floods have formed two alluvial side bars. The Rhône alluvial side bar is mainly composed of argillous alluvium and may be up to 1 km wide. The Séran side bar is more silty and its width ranges from 100 to 200 m. The water table is level with the peat surface in the middle of the marsh. The water mainly originates from the neighbouring mountains, as revealed by numerous exurgences and resurgences. The vegetation is strongly influenced by the depth of the water table and the substrate composition. Crops are grown in the north, in the vicinity of the Rhône. A remnant of the original fluvial forest occupies the southern part of the Rhône side bar (Lavours Forest). A typical alluvial forest occupies the banks of the Séran. This forest is characterized by *Alnus glutinosa*, *Acer campestre*, *Fraxinus excelsior*. Some *Quercus robur* may be found on the outcrops. To the east, the forest is gradually replaced by a moor with *Salix cinerea*, *Betula verrucosa* and *Alnus glutinosa*. The moor then becomes more open with *Frangula alnus*, *Carex elata*, *Molinia coerulea* and *Filipendula ulmaria*. The central area of the marsh

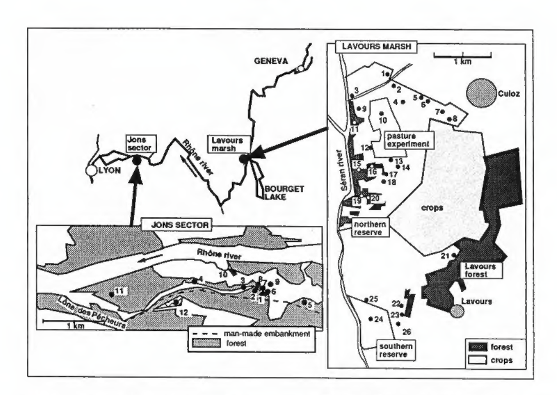


Fig. 1. — Geographic situation of studied sectors and studied sites. Sites in the Jons sector : 1, 2, 3, 4: Lône des Pêcheurs oxbow lake; 5, 10, 11: permanent ponds; 6, 7, 8, 9, 12: temporary ponds. Sites in the Lavours marsh: (1) sites in closed habitat: 11, 19: puddles; 15: drain; 16: peatbog; 20: Séran oxbow; (2) sites in open habitat: 2, 3, 4, 9, 10, 12, 13, 24: puddles; 1, 5, 7, 14, 21, 25: drains; 6, 8, 17, 18, 22, 23: peat excavations.

is occupied by the peat-bog characterized by *Schoenus nigricans* and *Cladium mariscus*. The vegetation was for a long time influenced by hay exportation, which hampered the colonization of the marsh by trees. Over the last thirty years, hay exportation has gradually disappeared and *Alnus glutinosa* is now observed everywhere. Crop covers a third of the total marsh area. Another third is managed as a Natural Reserve. It concerns the north-western part of the marsh (northern reserve) and a plot of land in the south-western part (southern reserve). Several experiments, including pasturing by horses and Highland Cattle in an enclosure, have been carried out to restrict colonization by the forest. At present, the rest of the marsh is managed according to traditional agricultural practices.

Twenty-six aquatic sites were visited during the spring of 1987 and 1991 (fig. 1). These sites were classified according to their shape and to their degree of cover as follows :

(1) Temporary ponds or puddles. These shallow sites with very gentle slopes were sampled in both open and covered environments. The density of aquatic vegetation in these ponds depended on the cover. In a forest, they were, for instance, vegetationless ruts

in pathways. In the open marsh, they might also be ruts, or natural depressions in the peat where underground water appeared. In most of them, water was not permanent, the lowering of the water table causing most of the puddles to dry up at the end of July. The watertight bottom of the covered sites and their protection from sunlight ensured longer water retention, as confirmed by the presence of dense colonies of *Tubifex*.

(2) Drains. A dense network of man-made drains criss-crosses the whole marsh. In most of them, the water was almost stagnant and the banks abrupt. The connection of these drains with the Rhône or the Séran made fish colonization possible, especially by sticklebacks (*Gasterosteus aculeatus*).

(3) Large ponds. Their origins are diverse:

(a) In the open marsh, they are remains of peat excavations. The largest one, named Etang Delastre, measures 2 ha, but the area of some of them does not exceed a few square metres. They may be several metres deep and their banks are always abrupt. They are colonized by *Nymphea alba*.

(b) In the Séran alluvial side bar, an old oxbow lake is semi-permanent and 1.5 m deep when filled, with gentle slopes. Its vegetation is diverse (*Glyceria stagnatilis*, *Nymphea alba*, *Nuphar luteum*).

The Jons sector

The Jons sector is situated approximately 80 km downstream from the Lavours marsh. Numerous oxbow lakes and side arms in this sector are the remains of former meanders (Juget et al., 1976). The present study took place along a partly-closed side arm named "Lône des Pêcheurs", which opens into the river downstream. Several hydrobiological studies have been carried out on this arm (Juget et al., 1976, 1979). Twelve study sites were selected. Six of them (J6 to J11), located in the stretch of land between the arm and the Rhône, are overflowed almost annually. Sites J6, J7 and J8 were relatively silted, and retained water throughout spring. Their banks were colonized by *Phalaris arundinacea*. J9 was a recent unsilted and vegetationless depression in the pebble bed, with great variations in water level, in relation with the discharge of the river. J10 and J11 were deep and large permanent ponds ringed with *Typha latifolia*. Five other sites (J1 to J5) were in the side arm bed. J5 was a pond located underbush and isolated 100 m upward from the side arm, whereas the others (J1 to J4) were located properly in the side arm. One site (J12) lies on the land side of an embankment, which prevents it from being overflowed. This site only contains groundwater. The terrestrial environment of all these sites ranges from a moorland with willows of the *Salix cinerea* group to an alluvial forest with *Alnus glutinosa*, *Salix alba* and *Populus nigra* on the more elevated bars.

Methods

The sites were visited from two to four times during spring. Adult anurans were detected both visually and by listening. Amphibian larvae and adult newts were sampled with a landing-net. Abundance was arbitrarily estimated according to a semi-quantitative

scale with four levels : 0 = absence, 1 = only one observation of a given taxon; 2 = taxon observed several times in the site but irregularly; 3 = regular and numerous observations in the site. When small and close to one another, sites of the same type were grouped as one site in the results. In order to draw an overview of the amphibian fauna in the alluvial valley, an index of presence was computed as follows: for a given habitat type *i*, the presence index $P(i)$ of a taxon was: $P(i) = \Sigma_i(a \times n_i) / N_i$, where *a* is the abundance of the taxon estimated with the scale described above, n_i is the number of sites where the taxon was present and N_i the total number of sites in category *i*.

In France, discrimination among green frog taxons is not possible on the basis of morphological characters because of the undisrupted distribution of parameter values from *Rana lessonae* to *Rana ridibunda* pure types (ZUIDERWIJK, 1980; H. G. TUNNER, pers. comm.). The determination of *Rana ridibunda* was only accepted on the basis of calling according to the guide of GUYÉTANT & ROCHÉ (1987) or on basis of colour and shape of metatarsal tubercule according to ARNOLD, BURTON & OVENDEN (1978). *Rana lessonae* and *Rana* kl. *esculenta* could not be distinguished by means of biometry. Consequently, they are grouped under the name *Rana "esculenta"*. When precise determination of green frog was not accomplished, the term *Rana* synkl. *esculenta* was used (see DUBOIS & GÜNTHER, 1982).

In addition to the author's own observations, this study includes those of Yves MAJCHRZAK, Alain MORAND and Hubert TOURNIER.

RESULTS

LAVOURS

At Lavours, 10 taxons were observed (11 if *Rana "esculenta"* and *Rana ridibunda* are discriminated) (Table I). The highest richness (7 taxons) was reached in the puddles in an open environment. Among these puddles, the richest site (6 taxons) was pool L3. The particularity of this site is its area, which is approximately 2 ha. The puddles in the southern reserve contained 4 taxons. The most frequent taxons in open environments were, in decreasing order, *Rana dalmatina*, *Rana* synkl. *esculenta* and *Triturus helveticus*. *Bufo bufo*, *Bufo calamita*, *Rana temporaria* and *Hyla arborea* were occasional in this type of site.

Triturus alpestris occurred in the Séran oxbow lake together with the three commonest taxons described above. This site was the only one in which this species was observed.

Most of the excavations were very poor, except for site L23, which was inhabited by 3 taxons: *Rana dalmatina*, *Rana* synkl. *esculenta* and *Bufo bufo*. Note that this site was the only man-made excavation in alluvium. The other excavations were in peat bogs and contained only one taxon, exceptionally two and sometimes none. *Rana* synkl. *esculenta* was the most regular taxon there. *Rana dalmatina* and *Hyla arborea* were only occasionally observed. Amphibians were rather scarce in drains where *Rana* synkl. *esculenta* was the most constant taxon. *Rana dalmatina* and *Triturus helveticus* occurred in drains when depth was less than 0.5 m.

Table I. — Abundance of amphibian taxons in the sampled sites (semi-quantitative scale)

	Jons sector												Lavours: closed habitat				
Habitat type	**Oxbow**				**Perm. ponds**			**Temporary ponds**					**Temp. ponds**		**Drains**	**Perm. ponds**	
Site number	**J1**	**J2**	**J3**	**J4**	**J5**	**J10**	**J11**	**J6**	**J7**	**J8**	**J9**	**J12**	**11**	**19**	**15**	**16**	**20**
T. helveticus					1			2	2	1		2					3
T. alpestris					1				2	2		2					1
B. variegata														2			
P. punctatus											2						
B. bufo														1			
B. calamita								2			2	3					
H. arborea								2				3					
R. temporaria					1			1	1	1			1				
R. dalmatina								3	2			3	2		1		2
R. synkl. *esculenta*	1	1	1	1		2	2	3	3	1		3	1	1	1	1	2

	Lavours: open habitat																				
Habitat type	**Temporary ponds**								**Drains**							**Excavations**					
Site number	**2**	**3**	**4**	**9**	**10**	**12**	**13**	**24**	**1**	**5**	**7**	**14**	**21**	**25**	**26**	**6**	**8**	**17**	**18**	**22**	**23**
T. helveticus		2		2			1				1		1	1							
T. alpestris																					
B. variegata																					
P. punctatus															1						
B. bufo		1																			2
B. calamita								1													
H. arborea		1																	1		
R. temporaria		2						1													
R. dalmatina	2	3	2	3	2	1		2												1	2
R. synkl. *esculenta*	1	2		1		1	3	3	1	1	1	2		1			1	2	3	1	1

The underbush puddles hosted some clutches of *Rana dalmatina*. Some puddles were inhabited by small groups of *Bombina variegata*, particularly in the Séran alluvial forest. These puddles were also colonized by juvenile *R.* synkl. *esculenta* in summer.

Figure 2 shows the dispersion of the different taxons over the marsh. *Rana dalmatina*, *Rana* synkl. *esculenta* and *Triturus helveticus* were the only ones to be distributed throughout the marsh. *Triturus alpestris*, *Bombina variegata*, *Pelodytes punctatus*, *Bufo bufo* and *Rana temporaria* were found only in the vicinity of forested areas. Data concerning *Bufo calamita* and *Hyla arborea* were scarce. Both species were found in the open marsh. When partial determination was possible within the *Rana* kl. *esculenta* synklepton, *Rana "esculenta"* was identified in shallow puddles near the pasture enclosure (L12, L13) whereas *Rana ridibunda* was found in deep drains near the forest (L17) and in large peat excavations (Etang Delastre: L18).

JONS

In the Jons sector, the amphibian fauna was similar to that observed at Lavours except for the absence of *Bombina variegata* and *Bufo bufo* (Table I). Highest richness was reached in temporary sites. Diversity and abundance were very low in permanent eutrophic ponds and in the side arm. In these sites, *Triturus helveticus* and *Rana* synkl. *esculenta* were the only nearly constant taxons.

J9 stood out among the temporary ponds as it hosted only *Bufo calamita* and *Pelodytes punctatus*. This site was characterized by its oligotrophy and short water retention. Both *Bufo calamita* and *Pelodytes punctatus* appeared in this site immediately after water rise.

As at Lavours, *Triturus helveticus*, *Rana dalmatina* and *Rana* synkl. *esculenta* were the most constant taxons in all the sites. However, they were more abundant in temporary ponds, where *Triturus alpestris* also occurred frequently. *Bufo calamita* and *Hyla arborea* were relatively more abundant at Jons than at Lavours.

HABITAT TYPES

When analysing presence indices, the site categories were reduced to the nine habitat types in Table I. Both taxons and habitat types were rearranged in order to bring together similar habitats and similar taxons (fig. 3).

The habitats were first classified according to cover. The less covered was the environment, the richer was the breeding amphibian fauna. Temporary ponds from the two sectors were the richest habitats, whereas the underbush drains and side arm contained the poorest fauna, with only two taxons. *Rana* synkl *esculenta*, *Rana dalmatina* and *Triturus helveticus* were the most constant taxons. In contrast, *Bufo calamita*, *Pelodytes punctatus* and *Hyla arborea* were mostly found in temporary ponds. *Bombina variegata* was characteristic of underbush temporary ponds.

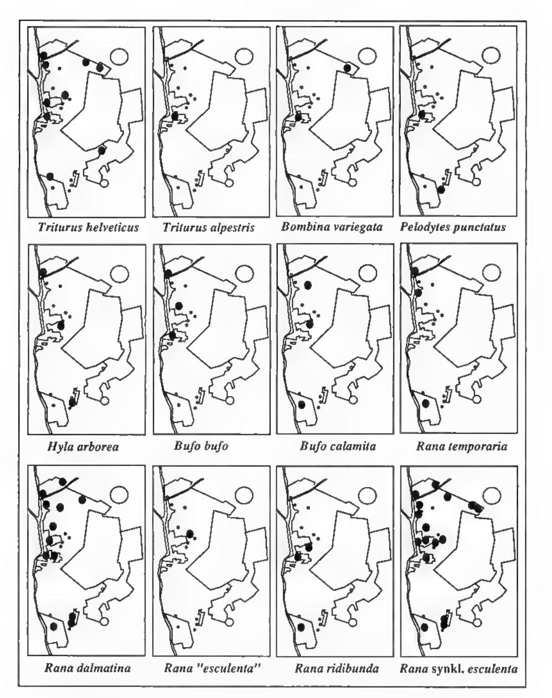


Fig. 2. — Dispersion of amphibian taxons over the Lavours marsh

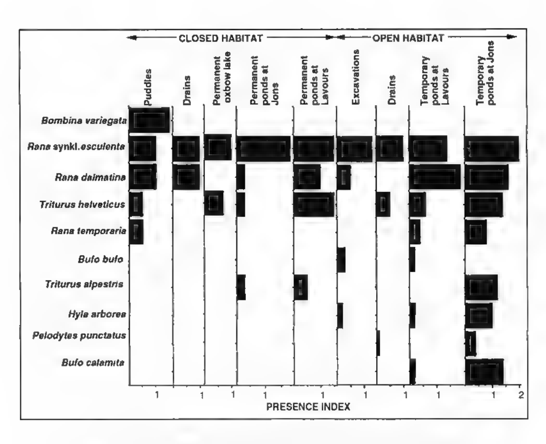


Fig 3. — Classification of both habitat types and taxons through ordering of presence index (see text)

Rana "esculenta" was identified only in very shallow pools of the peat bog at Lavours. *Rana ridibunda* was the only green frog found at Jons, both in temporary ponds and in deeper sites, such as the side arm and the regularly overflooded ponds J10 and J11. At Lavours, *Rana ridibunda* was less abundant and was identified in the large peat bog (L18), in large drains and in the Séran oxbow lake.

DISCUSSION

Both at Lavours and at Jons, highest richness was reached in temporary shallow ponds in open environments. Diversity and abundance of amphibians decreased as ponds became more covered or showed more abrupt slopes (as in drains or peat excavations). Amphibians also became scarce as fish became abundant, for instance in large deep ponds or in the side arm connected with the river. With regard to the floodplain typology of

Bravard, Amoros & Pautou (1986), great amphibian diversity is found in temporary functional units belonging to both plesiopotamic and paleopotamic functional sets. Juvenile temporary ponds in gravel beds highly influenced by river discharge are characteristic of the units of the plesiopotamic set. In the present study, they were represented by the temporary ponds at Jons and some sites (L3, L9, L24) near the Séran at Lavours. In contrast, temporary units of the paleopotamic set are mature sites mildly influenced by river discharge, such as sites L2, L4, L10, L12, L13 at Lavours.

Triturus helveticus, *Rana dalmatina* and *Rana* synkl. *esculenta* form a group of taxons that is frequently observed in the south-east of France where it may be regarded as the basis of the amphibian fauna (Zuiderwijk, 1980). Therefore, these taxons are not characteristic of the floodplain. Because of its small body size, *Triturus helveticus* occupies a rather small spatial niche restricted to gently-sloping banks rich in vegetation. It may be considered as a dispersive pioneer species because its range of aquatic sites is broader than that of other taxons (unpubl. data). In the study area, the coexistence of *Rana dalmatina* and *Rana* synkl. *esculenta* may be the consequence of niche partitioning. *Rana dalmatina* is a precocious breeder that spawns at the beginning of March, while *Rana* synkl. *esculenta* spawns from the end of April to the beginning of June. When reproduction occurs in the same site, *Rana dalmatina* tadpoles develop before those of *Rana* synkl *esculenta*, provided that water temperature is sufficiently high to allow their metamorphosis before June. Such a succession can be observed when the environment receives sufficient sunlight. Except during the breeding period, adults of *Rana dalmatina* were predominantly observed in the alluvial forest, where their life is terrestrial. Inversely, *Rana* synkl. *esculenta* inhabits pond banks and is typically amphibious. At Lavours, it is noticeable that *Rana dalmatina* breeds on the first days of mild weather in sites which can be up to 1 km from the forest, suggesting that frogs hibernate either in or near such sites.

In contrast to the first group of taxons, *Bufo calamita*, *Pelodytes punctatus* and *Hyla arborea* are characteristic of shallow temporary ponds. This group of species was also found frequently in isolated puddles in large riverbeds along the Rhône in the vicinity of Montélimar (south of France) by Zuiderwijk (1980). In *Bufo calamita* and *Pelodytes punctatus*, the date of reproduction is not strongly determined by temperature or photoperiod but may occur over a long period of time (Diaz-Paniagua, 1986, Sinsch, 1988) These species may adjust their breeding date to temporal variations of pond filling, that depend on relatively unpredictable river discharge. On the other hand, in these species, the diet of the tadpoles can be more diversified than in other species because of both behavioural and anatomical adaptations (Diaz-Paniagua, 1985, 1989, Viertel, 1987, 1990). Consequently, we may assume these species to be more efficient in exploiting oligotrophic sites and regard them as typical of the floodplain.

Rana temporaria, *Bufo bufo*, *Triturus alpestris* and *Bombina variegata* were always found in the close vicinity of forest areas. These species become abundant and dominant in the forested hills surrounding the river. In the floodplain, they seem to colonize the more elevated parts of the alluvial forest.

Among the 14 amphibian taxons of the French Upper-Rhône region (Castanet & Guyétant, 1989), 11 were found in the floodplain. The missing species were *Salamandra salamandra*, *Triturus cristatus* and *Alytes obstetricans*. Reproduction of both *Salamandra*

salamandra and *Alytes obstetricans* has evolved towards a greater independence from the aquatic environment (ovoviviparity for *Salamandra*, egg carrying for *Alytes*), their fecundity is low We may assume that the selective pressures which led to such an adaptation to terrestrial life also involved the loss of capacity for aquatic life. The absence of these species from the regularly overflowed area may be a consequence of intolerance to prolonged submersion. The causes explaining the absence of *Triturus cristatus* may be different This species chooses deep (depth > 1 5 m) fish-free ponds for breeding (DOLMEN, 1988; PAVIGNANO, 1989). In the alluvial valley, most of the deepest ponds do not dry up because of the high level of the water table and many fish remain in such sites after floods (COPP, 1989). The occurrence of convenient ponds for *Triturus cristatus* is more likely outside the flooded area.

In a braided or anastomosed sector of the floodplain, the semi-aquatic sites may be classified according to a gradient of river influence from the active channel(s) to the floodplain borders. The mechanical impacts of floods (by erosion and sedimentation) are more intense in the vicinity of active channels, where pond turnover is expected to be relatively rapid (less than 10 years). The bottom of such ponds is not silted, which leads to relatively unpredictable water filling depending on river discharge. The mechanical impact of the floods decreases as the distance from the active channel increases. On the border of the floodplain, natural ponds are formed by oxbow fragmentation following filling up with both sediment and organic matter. The same mechanism also leads to the disappearance of ponds. This process may be slackened by underground water exurgence. Such ponds may persist for several decades. Their bottom is silted by inorganic and organic matter, leading to a retention of both flood- and rain-water during several months. The sites close to the river are characterized by high temporal and spatial variability, whereas those at the border of the floodplain (last stages of the paleopotamon) show a greater stability, both within space and time. According to the patch dynamics concept (TOWNSEND, 1989), the first type should host communities whose principal mode of regulation lies in colonization processes, whereas the second type should be inhabited by competition-regulated communities. The present data partially corroborate this model and lead us to the following assumptions *Bufo calamita*, *Pelodytes punctatus*, *Rana ridibunda*, and, to a smaller extent, *Hyla arborea*, may be considered as pioneer species *Rana dalmatina*, *Rana* synkl *esculenta*, *Bufo bufo* and *Rana temporaria* may coexist in more stable ponds, where niche partitioning occurs among tadpoles. At the end of the aggrading process, when depth becomes very shallow, water presence becomes temporary. This last stage may be colonized by *Bombina variegata*, a site-faithful species with spawning-date flexibility (BARANDUN, 1990). These assumptions and the validity of the patch dynamics concept will be the basis of a detailed study of amphibian communities in the French Upper-Rhône floodplain.

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Prey choice behaviour in light and darkness in a facultative cave dweller, the Pyrenean salamander *Euproctus asper*

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In prey choice experiments, seven larvae of the Pyrenean salamander, *Euproctus asper*, were confronted in light and in darkness with two glass microaquaria each filled with either 10 dead or 10 living chironomids. One longside of each microaquarium was closed with a net to allow the free exchange of water with the surroundings. In light, all seven *E. asper* chose the microaquarium containing the living chironomids. During prey choice, one individual directed the snout at the net. All others directed their snouts either at one of the glass walls or at the mirror image produced by the chironomids underneath the microaquarium. In darkness, all *E. asper* located the prey with three individuals choosing the living and four choosing the dead prey. All individuals directed their snouts at the net. *E. asper* prey choice behaviour in light is clearly dominated by vision. In darkness, this facultative cave dweller forages successfully but is less choosy than permanent cave dwellers.

Introduction

When offered a choice between prey types with differential activity, predators frequently prefer the more active ones (e.g., Freed, 1980). Active prey provide additional visual, mechanical, and chemical cues reducing search times and enhancing the foraging efficiency in visually as well as in non-visually hunting predators (Martin, Witherspoon & Keenleyside, 1974; Hetherington, 1989; Uiblein et al., 1992). For instance, the blind cave salamander, *Proteus anguinus*, shows a significant preference for active prey if offered a choice between water conditioned with dead and living chironomid larvae (Durand, Parzefall & Richard, 1982). Under the same conditions however, the epigean salamander *Necturus maculosus*, the closest relative of *Proteus*, showed no significant preference (Durand, Parzefall & Richard, 1982).

The Pyrenean salamander *Euproctus asper* facultatively lives in caves (Clergue-Gazeau, 1971) and adjusts behaviourally both to epigean and hypogean foraging conditions. Experimental exposure to living or dead chironomids in light or darkness showed that *E. asper* detects and captures living prey in light faster than dead prey in light

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or living prey in darkness (UIBLEIN et al., in press). In light therefore, *E. asper* should prefer living to dead chironomids. In darkness however, foraging efficiency is reduced and living prey may be less preferred.

The preference for living prey in light and in darkness was tested experimentally confronting *E. asper* with a choice between living and dead chironomids.

MATERIAL AND METHODS

Seven larvae of *Euproctus asper*, two years old and with total lengths between 31 and 37 mm, were tested individually. All experimental animals had former feeding experience with living and dead chironomids and had been reared in the cave of the Laboratoire Souterrain du C N.R.S. at Moulis, France, under controlled conditions. The experiments were also carried out in that cave between 10.00 and 20.00 h and at a constant temperature of 11°C.

180 minutes before the experiments started, one hungry *E. asper* (four days without food) was introduced into the experimental glass tank (30 × 15 × 20 cm height). At the same time, two empty glass microaquaria (48 × 20 × 28 mm height) used in the subsequent choice experiments were added to accustom the animal to the test conditions. One longside of each microaquarium was closed with a fine net (fig. 1) to allow the free exchange of water with the sourroundings. One broadside had a small slot for introduction and extraction of chironomids. This slot could be tightly closed by a rubber plug (fig. 1).

Before the experiments started, the microaquaria were removed and filled each with either ten living or ten dead chironomid larvae (freshly killed by deepfreezing and then defrosted). Then the microaquaria were put back into the experimental tank at opposite positions and at a distance of 11 cm between each other with the side covered by the net directed towards the center of the tank. A distance of at least 7.5 cm was left between the microaquaria and the margins of the tanks. The lateral positions of the microaquaria (either left or right) were determined by a random pattern.

Each experimental animal was tested in two successive experiments, one in weak light (3 lux), and one in complete darkness. In the latter experiment, the observations were done with an infrared equipment (UIBLEIN et al., in press). The experiments started immediately after introduction of the microaquaria filled with chironomids into the experimental tank. With regard to the low sample size (n = 7), the following strict criterium (examined by preliminary testing) was used to determine a clear choice: the salamander remains with the snout in close contact with one of the walls of one microaquarium for at least one minute. For each choice, three alternative orientations of the snout were recorded (fig. 1): (1) the snout remains at the net; (2) the snout remains at one of the glass walls; (3) the snout remains at one of the side walls with the head held down and the snout directed at the mirror image produced by the chironomids underneath the microaquarium. In addition, the time period between the start of the experiment and the first occurrence of a clear choice ("latency"), and the number of snaps directed at the respective microaquarium were recorded.

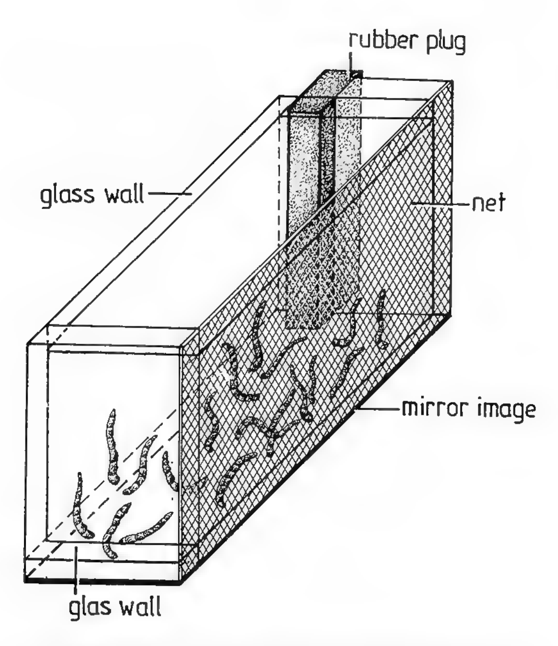


Fig. 1 Scheme of the type of glass microaquarium used in the choice experiments. The three possible orientations of the snout during prey choice are indicated.

Results

In light, *E. asper* showed a significant preference for living prey. All seven individuals chose the microaquarium with the living chironomids (P = 0.008, one-tailed binomial test [Zar, 1984]; Table I). The mean latency was 9.24 mn. The salamanders showed interindividual differences in snout orientation during prey choice (Table I): one individual directed the snout at the net, three individuals directed the snout at one of the glass walls, and three individuals directed the snout at the mirror image of the chironomids underneath the side with the net. All seven individuals held their positions for at least one minute with five of them snapping at a rate of between one and ten snaps per minute (Table I).

Table I. – Choice of prey type, latency, orientation of the snout, and number of snaps per minute in light (L) and in darkness (D). Seven *Euproctus asper* (a-g) were tested individually in two successive experiments. See text for further explanations.

	Prey type chosen		Latency (mn)		Snout orientation		Snaps/mn	
	L	D	L	D	L	D	L	D
a	living	dead	17.67	11.42	mirror	net	0	2
b	living	dead	9.77	16.35	mirror	net	1	0
c	living	living	19.13	27.88	glass	net	4	0
d	living	dead	1.33	7.53	mirror	net	0	0
e	living	dead	9.40	52.67	net	net	2	0
f	living	living	5.68	6.78	glass	net	2	4
g	living	living	1.67	2.97	glass	net	10	6

In darkness, no significant preferences for either prey type were detected with three individuals choosing living chironomids and four selecting the dead ones (P = 0.5, one-tailed binomial test; Table I). The median latency was 17.94 mn. Six of the seven *E. asper* showed longer latencies in darkness than in light (Table I). For the total set however, no significant differences between latencies in light and darkness could be detected (P = 0.09, Wilcoxon test [Campbell, 1989]). All seven individuals directed their snouts at the net during prey choice (Table I). This is significantly different from the number of individuals at the net in light (P = 0.002, Fisher's exact test [Sokal & Rohlf, 1981]). Three individuals showed a snapping response (Table I), which is not significantly different from to the number of individuals snapping in light (P = 0.3, Fisher's exact test).

DISCUSSION AND CONCLUSION

In light, *E. asper* clearly preferred the living chironomids showing a choice behaviour guided mainly by vision. Only one of the seven individuals tested directed the snout at the net. Three individuals approached the microaquarium at the side with the net but oriented their snouts at the mirror image instead of maintaining a multisensory contact with the chironomids at the net. These data are in accordance with earlier observations of *E. asper* foraging behaviour demonstrating the dominance of vision over non-visual perception in light (UIBLEIN et al., in press).

In darkness, all *E. asper* located the chironomids and showed a clear choice within several minutes. However, no consistent preference for either prey type was detected. *E. asper* lives in caves only facultatively and may be less sensitive to non-visual prey cues than permanent cave dwellers. *Proteus anguinus*, for instance, approaches living chironomids in darkness significantly faster than *E. asper* (UIBLEIN et al., in press) and clearly preferred living to dead prey in choice experiments (DURAND, PARZEFALL & RICHARD, 1982; UIBLEIN & PARZEFALL, in press). A similar choice behaviour has been found in a cave dwelling population of the fish *Astyanax fasciatus* (KLIMPEL & PARZEFALL, 1990).

A first crucial step towards efficient predation in caves is the shift from a visually directed to a more "widely", chemically and mechanically guided foraging mode (UIBLEIN et al., in press). A second step may be to choose those prey types which can be approached faster and are more profitable in terms of nutritional quality. *E. asper* is capable of performing the first step at present (UIBLEIN et al., in press). However, no indications have been found that this species may also realize the second step (see also LENGVENUS & PARZEFALL, 1992). To further evaluate the current status of *E. asper* adaptation to cave foraging conditions, a thorough comparison of the behavioural ecology of epigean and cave populations is needed

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Microscopía electrónica de barrido del aparato bucal de las larvas de *Melanophryniscus stelzneri* (Weyemberg, 1875) (Anura, Bufonidae)

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Scanning electron microscopy shows that the buccal apparatus of *Melanophryniscus stelzneri stelzneri* (Anura, Bufonidae) larvae has a well developed horny beak with teeth with large main cusp, multicusped labial teeth with 10 to 12 denticles in each paddle, paddles with short necks, and an oral disc with only few (12 to 16 on each side) supramarginal and inframarginal conical papillae.

Introducción

Fernandez (1927) efectuó por primera vez una descripción general de la morfología del aparato bucal externo de la larva de *Melanophryniscus stelzneri* (Weyemberg, 1875) (Anura, Bufonidae), observando que la disposición de las hileras de dientes labiales o queratodontos determinaban la fórmula dentaria 2/3. Gallardo (1987) coincide con Fernandez (1927) en la distribución de las hileras dentarias Basándose en datos recopilados por Cei (1980), Altig & Johnston (1986) organizaron la descripción sintética de la anatomía externa revelada por el microscopio estereoscópico.

Prigioni & Langone (1990) destacan la existencia de diferentes formas de distribución de las hileras de dientes labiales en las larvas de tres especies del género *Melanophryniscus* y sólo efectúan una breve caracterización de la morfología de los rostrodontos y queratodontos en *Melanophryniscus orejasmirandai*

Las referencias acerca de la anatomía bucal de las larvas de *M. stelzneri stelzneri* son escasas (Fernandez, 1927; Cei, 1980), siendo nula toda referencia acerca de la conformación ultraestructural del aparato bucal.

El propósito de este trabajo es poner en evidencia la conformación anatómica de los componentes del disco oral de las larvas de *M. stelzneri stelzneri* que revela el microscopio electrónico de barrido, permitiendo mayor precisión en la descripción de algunos

caracteres larvales y contribuir así al conocimiento de la anatomía larval comparada con una nueva gama de caracteres morfológicos de posible aplicación taxonómica.

Materiales y métodos

Veinticinco larvas de *Melanophryniscus stelzneri stelzneri* fueron obtenidas en la provincia de Buenos Aires (Sierra de la Ventana), en la provincia de San Luis (Sierras de San Luis, El Trapiche) y en la provincia de Córdoba (Sierras de Córdoba, Dique Los Molinos; Tanti y El Tigre, Calamuchita).

Los ejemplares fueron fijados en Ancel y Vitemberguer (Rough, 1962) o formol al 4 % y al 10 %.

Se consideraron los ejemplares en los estadios con el aparato bucal completamente desarrollado y funcional (estadios 27 al 37, según Gosner, 1960). Se seleccionaron quince ejemplares para efectuar las observaciones con microscopio electrónico de barrido (MEB), y el resto se destinó para las observaciones con microscopio estereoscópico.

El tratamiento aplicado al material destinado a MEB fué basado en el método de Fiorito de Lopez & Echeverría (1984), pero en la mayoría de los casos no se llevó a cabo la desecación final al vacío, sino que se modificó para poder realizar una deshidratación lenta: (1) en alcohol etílico (70 %, 24 h; 80 %, 12 h; 96 %, 6 h; 100 %, 3 h); (2) en una mezcla de alcohol 100 % acetona, en distinta proporción: (a) 3:1, 3 h; (b) 1:1, 2 h; (c) 1.3, 2 h, (3) en acetona pura, por lo menos tres horas; (4) secado al aire y montaje.

En el caso que el material no quedara totalmente seco a los pocos segundos después de separarlo de la acetona, debió colocarse nuevamente en acetona pura durante una hora, como mínimo.

La terminología utilizada para la descripción del aparato bucal y de los dientes está basada en la propuesta por Van Dijk (1966), Altig (1970) y Deunff & Beaumont (1959).

Resultados

El disco oral presenta forma triangular cuando se halla en posición de descanso, con una brecha papilar dorsal y otra central muy amplias En la región comisural (o angular), el disco es emarginado. Presenta papilas marginales únicamente en la región comisural, dispuestas en dos grupos netos: suprangulares e infrangulares. Cada grupo está formado por seis a ocho papilas, y los grupos están separados por una emarginación profunda. Las papilas marginales son simples, cónicas, más largas que anchas y con borde libre liso (fig. 1).

No se hallaron papilas intramarginales.

El pico córneo está bien desarrollado y queratinizado con una coloración castaño oscuro o negro La porción superior forma un arco amplio y convexo. La porción inferior presenta una configuración en forma de V.

El pico córneo se muestra profundamente aserrado. Las piezas dentarias (rostrodontos) se disponen en empalizada, con la cúspide alargada (fig. 2). La altura de cada diente es, por lo menos, el doble del ancho de la base del mismo. En ejemplares correspondientes al estadio 28, se ha observado que cada diente del pico córneo puede alcanzar un largo máximo de tres veces el largo de su base. El ápice de cada rostrodonto puede presentarse agudo o romo (figs. 2 y 4).

Los pliegues labiales se diponen en cinco hileras. dos anteriores y tres posteriores, sosteniendo a los queratodontos y permitiendo el movimiento de las hileras de dientes. Las hileras A-1, A-2, P-1 y P-2 se extienden desde un extremo al otro de las márgenes laterales del disco. La P-3 es la hilera de menor extensión (fig. 1).

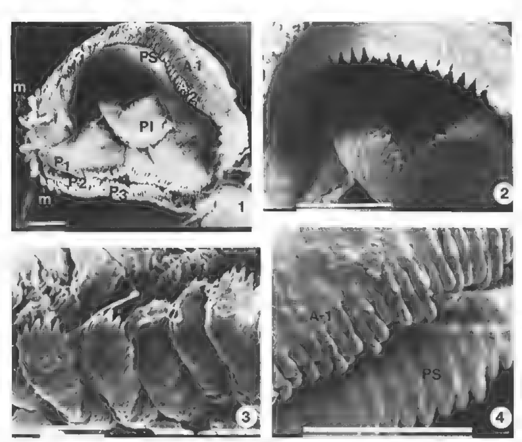


FIG. 1. — Vista general del aparato bucal de la larva de *Melanophryniscus stelzneri.* A-1, primera hilera anterior; A-2, segunda hilera anterior; P-1, primera hilera posterior; P-2, segunda hilera posterior, P-3, tercera hilera posterior; PI, parte inferior del pico córneo, PS, parte superior del pico córneo, m, papila marginal. Escala: 100 µm.

FIG. 2 — Detalle del pico córneo de la larva de *Melanophryniscus stelzneri.* Escala 100 µm

FIG. 3 — Queratodontos de la larva de *Melanophryniscus stelzneri.* Escala: 10 µm.

FIG 4 Queratodontos de A-1 de la larva de *Melanophryniscus stelzneri* por desprenderse y suprarostrodontos con ápices desgastados. Escala: 100 µm.

La distribución de hileras de queratodontos determina la fórmula dentaria 2/3. En sólo tres casos (en estadios 31, 32 y 33), se observó una pequeña escotadura mediana en la P-1 (fig. 1).

Cada vez que emerge una camada de queratodontos, ellos presentan una espátula corta pero más larga que ancha, con dentículos o cúspides en número variable de 10 a 12, generalmente con 6 a 8 cúspides centrales, bien desarrolladas y separadas. El cuello es corto (fig. 3). En los casos en que se observan aflorando dos camadas de dientes, una por debajo de la otra, los más distales pueden presentar el cuello alargado, pero nunca más largo que la espátula (fig. 4).

Los pliegues labiales soportan los queratodontos espatulados, presentan varias cúspides funcionales al mismo tiempo (aproximadamente entre 8 y 10) y con una proporción ancho máximo espátula / largo de espátula de 1/2.

Discusión

(1) Los caracteres morfológicos aquí descritos para la larva de *Melanophryniscus stelzneri stelzneri* determinan la fórmula dentaria 2/3 en coincidencia con Fernandez (1927) y con Garrido (1989) para *M. stelzneri montevidensis*.

Fernandez (1927) y Gallardo (1974) señalan que el pico córneo de las larvas de *M. stelzneri* es débil, quizás como sinónimo de pequeño, como lo describen Kehr & Williams (1990). En la muestra estudiada se observó que el pico córneo está bien desarrollado y queratinizado, pero es angosto en sentido anteroposterior.

Por otra parte, si tomamos a manera de ejemplo la extensión relativa que ocupa el pico córneo superior en el disco oral desde un extremo al otro, veremos que, en el caso de la muestra estudiada, representa el 50 % de la extensión total del disco tomada entre ambas comisuras, a nivel de las emarginaciones. En el caso observado por Fernandez (1927: 277, fig. 1), la distancia entre los extremos del pico córneo superior representa sólo el 33 %. Esta diferencia podría estar asociada con causas intrínsecas del único ejemplar estudiado por Fernandez y en cuyo diagrama se basan la mayoría de los autores que coinciden con ella.

(2) Las variaciones morfológicas detectadas en los rostrodontos y en los queratodontos no implican la existencia de heterodoncia dimensional permanente, sino que se deben al desgaste de los mismos.

A medida que los dientes afloran, envejecen: la espátula y el cuello se alargan, pudiendo cambiar la forma general hasta que se desprenden y caen. Esto fué comprobado anteriormente en *Bufo arenarum* (Echeverría et al., 1987; Fiorito de Lopez & Echeverría, 1989).

El grado de envejecimiento del diente aumenta con el tiempo de utilización del mismo; se pueden producir leves modificaciones en las piezas córneas, siendo más notables en los queratodontos que en los rostrodontos. En ellos las cúspides tienden a hacerse romas hasta que, a veces, sus extremos se acortan o se pierden. En los queratodontos el cuello puede alargarse y afinarse cuando están próximos a desprenderse.

Por ello, para poder obtener una fiel descripción de la morfología dentaria, será conveniente tomar como base de referencia a las piezas dentarias observadas en los estadios 25 o 26 y en aquellos inmediatamente después de cada recambio. Es decir, cuando aflora la primera camada de queratodontos, o eliminando mecánicamente los dientes modificados, para hallar los que se encuentran inmediatamente debajo de ellos, que conservan intacta la morfología original.

(3) En cuanto a la escotadura detectada en la P-1, considero que es probable que ésta sea una disposición transitoria y que esté relacionada con el crecimiento del aparato bucal, en especial de los pliegues labiales que contienen las columnas de dientes en desarrollo, como es el caso de *Bufo arenarum* (FIORITO DE LOPEZ & ECHEVERRÍA, 1989).

(4) La forma general de los dientes labiales se acerca, por ejemplo, a la observada por FIORITO DE LOPEZ & ECHEVERRÍA (1984) en *Bufo arenarum*, de amplia distribución en la Argentina, que, en la época de reproducción, frecuenta aguas quietas permanentes o semipermanentes.

En las larvas de *M. stelzneri stelzneri* examinadas, la posición de los queratodontos y de las cúspides de los mismos se presentan marcadamente curvados hacia la región bucal (más pronunciado se observa en las hileras posteriores). Esto podría estar asociado al tipo de captura del alimento que llevan a cabo, por raspado o rastrillado, reteniendo el alimento y acumulándolo entre las hileras (dientes tipo *Rana*, según ALTIG & JOHNSTON, 1989).

La forma de V del pico inferior podría contribuir al corte y/o retención de restos vegetales, frústulos de diatomeas, etc., como se estima que ocurre en otras especies.

Llama la atención que, en la porción anterior del intestino, se hallaron largos frústulos (de más de 200 µm) y partes rotas (de aproximadamente 100 µm) de diatomeas planctónicas como *Synedra ulna* y su forma de resistencia, quizás recogidos del fondo del cuerpo de agua semipermanente con corriente intermitente. Es posible que por la morfología del pico córneo superior, que permite una abertura bucal amplia, quede facilitado el ingreso a la cavidad bucal de estructuras rígidas como los largos frústulos o las diatomeas vivas de *Synedra ulna*, en gran cantidad y enteras.

Considerando que en un cuerpo de agua las fuentes de alimentos pueden ser varias y que cada una de ellas está sujeta a ciclos biológicos, si los renacuajos de *M. stelzneri* se comportaran como oportunistas alimentarios, y de acuerdo con la morfología bucal ya comentada, tendrían fácil acceso a alimentos de gran tamaño que quizás provean en conjunto, mayor contenido calórico útil para el desarrollo que, según FERNANDEZ (1927), es rápido.

CONCLUSIONES

(1) Los queratodontos tienen espátulas cortas, con 10 a 12 dentículos o cúspides, generalmente con 6 a 8 cúspides centrales bien desarrolladas y separadas. El cuello es corto.

(2) El pico córneo es bien desarrollado y queratinizado, profundamente aserrado.

(3) Hay escasas papilas, sólo marginales, comisurales (12 a 16 por lado).

(4) Las variaciones morfológicas en los dientes se deben al desgaste.

(5) La fórmula dentaria observada es 2/3.

Resumen

El aparato bucal de las larvas de *Melanophryniscus stelzneri stelzneri* presenta un pico córneo bien desarrollado y queratinizado. Los rostrodontos son unicuspidados, con cúspides pronunciadas. El infrarostrodonto presenta una configuración en V en estado de reposo y es poco visible. El suprarostrodonto es convexo, muy extenso.

Los dientes labiales son espatulados, multicuspidados (10 a 12 cúspides), con cuello corto, nunca más largo que la espátula. Hay papilas comisurales únicamente, inframarginales y supramarginales, desde 12 hasta 16 por cada lado.

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